

Visual Ageing: Unspecific Decline of the Responses to Luminance and Colour

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We have investigated whether ageing affects selectively the responses to equiluminant patterns of pure colour contrast. In two groups of subjects (mean ages 29 and 72 yr) contrast thresholds were measured psychophysically for the detection and for the discrimination of the direction of motion of drifting gratings. The gratings were modulated either in pure luminance contrast (and uniform colour), or pure chromatic contrast (red-green equiluminant gratings). In subjects of the same age groups, visual evoked potentials (VEP) were recorded in response to gratings with either pure luminance contrast or pure colour contrast sinusoidally reversed in contrast at various temporal frequencies. It was shown that psychophysical contrast sensitivity for equiluminant patterns deteriorates significantly with age, and VEP latency increases. However, these effects of ageing on the responses to patterns of pure colour contrast are substantially the same as those observed in the same subjects for stimuli with pure luminance contrast. The results suggest that ageing causes a small and unspecific decline of the response of the visual system to luminance and colour contrast. Copyright © 1996 Elsevier Science Ltd.

Ageing Colour Motion Evoked-potential Spatio-temporal frequency

INTRODUCTION

A number of psychophysical studies indicate a loss of spatio-temporal contrast sensitivity with ageing, although there is still some controversy about the ranges of spatial and temporal frequencies that are affected by age and about the relative roles of optical and neural factors. However, it seems clear that the decline in contrast sensitivity occurs primarily for middle and high spatial frequencies and that there is a loss in temporal resolution for luminance modulated uniform fields (Wright & Drasdo, 1985; Tyler, 1989; Kim & Mayer, in Spear, 1993). With counterphase modulated or drifting sinusoidal gratings a loss of contrast sensitivity with ageing occurs even at low temporal frequencies, particularly at relatively high spatial frequencies [Tulunay-Keesey et al. (1988); Nameda et al. (1989); Elliott et al. (1990); see Spear (1993) for a recent review]. Motion sensitivity, as tested with random dot moving patterns, also decreases progressively with age (Ball & Sekuler, 1986; Trick & Silverman, 1991).

Pattern visual evoked potential (VEP) studies show that the latencies of responses to contrast reversal of highcontrast checkerboard or sinusoidal gratings increase with age [see Spear (1993) for review], and there is evidence that this effect occurs primarily at high spatial and low temporal frequencies (Porciatti *et al.*, 1992). At relatively low temporal frequencies the VEP amplitude is also reduced.

Various studies on visual ageing have tried to answer the question whether there is a selective deterioration with ageing of one or the other of the two main neural pathways, the P and the M pathway [see Spear (1993) for review]. Given the roles played by the two pathways in the visual system of non-human primates, a deterioration of responses in the high-spatial and low-temporal frequency domain would suggest a selective deficit in the P stream, while the loss of motion sensitivity would suggest an age-related decline of functions in visual cortical areas that receive their major input via the M stream [see Merigan & Maunsell (1993) for review].

In the monkey, sensitivity to colour contrast is subserved by the P pathway (Merigan & Maunsell, 1993). Measuring colour-contrast sensitivity with equiluminant stimuli may therefore offer an opportunity to investigate whether, in humans, ageing affects selectively the neural pathway primarily responsible for the responses to pure chromatic contrast.

The sensitivity to chromatic contrast in equiluminant patterns (e.g. red-green equiluminant gratings) is known to have different spatial and temporal characteristics compared with the sensitivity to luminance contrast. In

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particular, the spatial and temporal resolution is lower for equiluminant gratings (Kelly, 1983; Mullen, 1985). The perception of motion is weak for stimuli of pure colour contrast (Cavanagh et al., 1984; Troscianko, 1987; Troscianko & Fahle, 1988; Cavanagh & Anstis, 1991; Mullen & Boulton, 1992) and the contrast threshold for the discrimination of motion direction at equiluminance at relatively low temporal frequencies is higher than detection threshold (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Mullen & Boulton, 1992; Derrington & Henning, 1993; Palmer et al., 1993; Gegenfurtner & Hawken, 1995), whereas at higher temporal frequencies the discrimination and detection thresholds converge. For luminance contrast, the direction of motion can usually be discriminated at detection threshold, at all temporal frequencies (provided that the exposure is not too brief).

We have investigated whether the contrast sensitivity for equiluminant red-green drifting gratings and the amplitude and latency of the VEP responses to contrastalternating equiluminant gratings were selectively affected by age. Contrast thresholds for the detection and for the discrimination of motion direction have been measured psychophysically in two groups of subjects (17-35 and 63-84 yr old, respectively) with either pure luminance contrast (and uniform colour), or pure chromatic contrast (red-green equiluminant gratings). In subjects of the same age groups, VEPs were recorded in response to gratings with either pure luminance contrast or pure colour contrast (with contrast scaled at a fixed amount above threshold) reversed in contrast at various temporal frequencies. The findings show that age affects both psychophysical contrast sensitivity and VEP latency for red-green equiluminant patterns, but the effects of ageing on the responses to patterns with pure colour contrast are not significantly different from those observed in the same subjects for stimuli with pure luminance contrast.

Stimuli

The stimuli were horizontal sinusoidal gratings of spatial frequency 1 c/deg, modulated either in luminance (yellow-black) or in chromaticity (red-green), made by adding red and green sinusoidal patterns (in-phase for the luminance patterns and out-of-phase for the chromatic patterns). The instantaneous luminances of the red and green guns ($L_R(y,t)$ and $L_G(x,t)$) were given by:

$$L_{R}(y,t) = rL_{0}\left\{1 + 0.5a \cdot \exp\left(\frac{-t^{2}}{2\sigma^{2}}\right) \cdot \cos[2\pi(f_{s}y + f_{t}t)]\right\}$$
$$L_{G}(y,t) = (1-r)$$

$$\times L_0 \left\{ 1 + s \cdot 0.5a \cdot \exp\left(\frac{-t^2}{2\sigma^2}\right) \cdot \cos[2\pi(f_s y + f_i t)] \right\}$$
(1)

where r is the colour ratio, the ratio of red to total luminance, L_0 mean luminance, a amplitude, f_s spatial frequency and f_t temporal frequency of drift. $s = \pm 1,+1$ for the luminance condition (yellow-black), and -1 for red-green equiluminance (for appropriate r). Each presentation was vignetted within a gaussian window of standard deviation s = 200 msec.

The gratings were generated by a specialized grating generator (Cambridge Research VSG2/2) and displayed on a colour monitor (Barco CCID 7751) with 14 bit resolution at 120 Hz, 512 lines per frame. The display was viewed through yellow filters (Kodak wratten 16) to attenuate wavelengths <500 nm that are relatively more absorbed by the eye lens in old subjects (Ruddock, 1965; van den Berg & Ijspeert, 1995). Viewed through the filter, CIE co-ordinates were x = 0.65, y = 0.35 for the red phosphor, x = 0.39, y = 0.60 for the green. Meanluminance was 14 cd/m^2 . The gratings were masked by white cardboard to a square field of 25 cm side, subtending 14×14 deg from the viewing distance of 100 cm. The cardboard was floodlit to a mean luminance of about 7 cd/m^2 . For the main experiments, the chromatic stimuli were equiluminant for each subject, as judged by minimum sensitivity for a 15 Hz counterphased grating.

The subjects fixated a black spot at the centre of the screen. No artificial pupils were used (see Fig. 4 for pupil sizes). For the psychophysical experiment viewing was binocular and the gratings drifted upwards (for the detection task) or in either direction (for the discrimination task). For the VEP experiment viewing was monocular and the gratings either sinusoidally contrast-reversed at various temporal frequencies (steady-state VEP) or square wave reversed at 1 Hz (transient VEP).

Measurement procedures

Following the procedure introduced by Mullen (1985) the ratio of colours [r in Eq. (1)] was varied by varying the relative luminances of the red and green stimuli. The ratio-of-red-to-total luminance (r) could be varied from 0 to 1, where r = 0 defined a green-black pattern, r = 1, a

METHODS Subjects Ten young subjects (mean age 29.1 yr, SD 5.3, four males, six females) and 10 elderly subjects (mean age 72.3 yr, SD 7.5, three males, seven females) were used for the psychophysical experiment. Two groups of subjects participated in the VEP experiment, 10 were

subjects participated in the VEP experiment, 10 were young (mean age 25.5 yr, SD 6.5, four males, six females) and nine elderly (mean age 71.5 yr, SD 9.1, three males, six females). Two of the young subjects and six of the elderly subjects participated in both experiments.

All subjects had a routine ophthalmological examination that excluded ocular diseases, including lens opacities. Refractive errors, when present, were less than 2 spherical and 1 cylindrical diopters, and were fully corrected. The corrected visual acuity was equal or better than 1.0. Informed consent was obtained from all observers after the nature of the technique and the aim of our research were fully explained. red-black pattern and intermediate values a red-green chromatic pattern.

Equiluminance was established for each subject by measuring contrast sensitivity with the method of ascending limits for a 1 c/deg red-green grating, counterphased at 15 Hz. For a given colour ratio [r of Eq. (1)], the experimenter decreased the contrast of the stimulus (without the gaussian temporal window) until the observer reported that the stimulus was no longer visible. The contrast was then lowered by 0.2-0.3 log units, and increased by 0.05 log unit steps until the subject reported seeing it, to yield threshold. Threshold was measured for several values of colour ratios over the range 0.1-0.9 with 0.1 steps over most of the range, decreasing to 0.025 near r = 0.5. At least two measures were made for colour ratios near r = 0.5. The point of minimum sensitivity was taken as the equiluminant value for the subject. Figure 1(A) shows an example of a sensitivity curve for one subject (in this case average of five threshold estimates per point) with a minimum sensitivity at ratio 0.47 (close to the V_{λ} equiluminance point).

The thresholds results of all other figures were obtained by a two-alternative, forced choice procedure. Here the stimuli were presented within a gaussian temporal envelope of 2 sec total duration, with time constant of 200 msec. Subjects were required to identify the direction of motion in a single presentation, or choose which of two tone-marked presentations contained the stimulus (the other was a blank screen of matched mean-luminance). The contrast of the stimulus homed in on threshold, guided by the adaptive QUEST procedure (Watson & Pelli, 1983).

The contrast sensitivity plotting in all the figures is relative to the physical contrast of the monitor guns, as there is still debate about the appropriate technique for calculating the effective chromatic contrast from the contrast of the individual cones (see for example Stromeyer *et al.*, 1985; Morrone & Bedarida, 1995). However, using the most standard method of calculating chromatic contrast, as the root-mean-square of the contrasts generated by the L and M cones, yields a measure of contrast for our stimuli that is a factor of 3.6 less than those shown in the figures. The luminance contrast remains unaltered.

VEP recording

EEGs were recorded with surface electrodes (O_z —right mastoid, ground left mastoid), pre-amplified 500fold, filtered between 1–100 Hz, re-amplified a further 100-fold, and fed into the D/A input (12 bit resolution, 2 kHz sampling) of a PC computer for real-time analysis. The computer averaged the EEG in synchrony with stimulus contrast reversal, and calculated second-harmonic amplitude and phase of the average (at least 250 events) by discrete Fourier analysis. To estimate background noise and artefacts, the computer also averaged on-line the EEG at a frequency 10% higher than the stimulation frequency, and calculated the second-harmonic amplitude of this average. For further details of chromatic VEPs, see Fiorentini *et al.* (1991) and Morrone *et al.* (1994).

As an independent measure of reliability, we calculated the standard error of our estimates of amplitude and phase from the two-dimensional scatter in amplitude and phase of the individual 40-sum packets.

RESULTS

Equiluminance

Figure 1(B) shows the equiluminant point evaluated by minimum sensitivity (see Methods, for all subjects, as a function of their age. For the older subjects, the average colour-ratio at equiluminance was 0.47, less than that for the young subjects (0.51), and less than the V_{λ} equiluminant point (0.50), indicating that they needed more green to produce equiluminance. This is to be expected from a yellowing of the lens, attenuating



FIGURE 1. (A) Contrast sensitivity as a function of colour ratio of a subject determined by the method of limits for a horizontal grating 1 c/deg sinusoidally reversed in contrast at 15 Hz. The colour ratio 0.47 at which contrast sensitivity was minimum was taken as the equiluminant value for this subject. The bars indicate standard error of the mean (average of five estimates).
(B) Equiluminant colour ratios of the ten young (○) and ten old subjects (●) participating in the psychophysical experiment, as a function of age. The arrows indicate the means of the two age groups.

selectively the shorter wavelengths, and quite consistent with available data (see Discussion.

Grating detection

Two distinct thresholds can be measured for moving stimuli: the threshold for discriminating the direction of motion (upward from downward in this case), and the threshold for detecting the pattern (discriminating it from a blank screen). Depending on the exact stimulus parameters, the two thresholds can separate in some conditions, particularly at low temporal frequencies (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Mullen & Boulton, 1992; Derrington & Henning, 1993; Palmer *et al.*, 1993; Metha *et al.*, 1994; Gegenfurtner & Hawken, 1995). We therefore measured discrimination thresholds over a range of temporal frequencies, but also detection thresholds at 2 Hz, where a large difference between the two types of thresholds may be expected (see Fig. 4, below).

Figure 2 shows colour against luminance contrast sensitivity for detecting a grating drifting at 2 Hz for the 10 older subjects (filled symbols) and the 10 young controls [see Fig. 1(B) for age distribution]. The two age groups form two distinct non-overlapping clusters, with poorer sensitivity and more scatter of the older group. The difference in the average sensitivities between the two groups (see arrows in Fig. 2) is not significantly different for luminance and colour patterns, being 0.23 (SE 0.04) log unit for luminance and 0.28 (SE 0.05) log unit for colour (the SE of the differences has been calculated as the square root of the summed variances of the log thresholds of the young and old subjects).

Discrimination of direction of motion

Contrast sensitivity for discriminating direction of motion was measured over a wide range of temporal frequencies. Figure 3 shows the averaged results of the 10 elderly (filled symbols) and 10 young (open symbols)



FIGURE 2. Colour contrast sensitivity plotted against luminance contrast sensitivity in the 2 Hz detection task, for the two groups of ten subjects each.



FIGURE 3. Mean contrast sensitivity of the two groups of subjects in the motion direction discrimination task plotted, for various temporal frequencies, for luminance (upper curves) and colour contrast (lower curves). The bars indicate the standard error of the mean (n = 10).

observers. For both luminance and colour contrast, sensitivity was less for the elderly subjects, by about 0.2 log units. A two-way ANOVA, performed separately for luminance and colour, showed that the reduction in sensitivity of the old subjects is statistically significant in both cases [luminance: F(1,79) = 52.5, P < 0.001; colour: F(1,59) = 63.2, P < 0.001]. However, the amount of loss in sensitivity varied little with temporal frequency: age by temporal frequency interactions were F(3,79) = 0.26, P = 0.85 for luminance; and F(2,59) = 0.4, P = 0.67 for colour.

The difference in mean contrast sensitivity of the old and young groups averaged over all temporal frequencies, was about 0.2 log units (SE 0.084) for luminance and 0.27 (SE 0.097) for colour, with standard errors evaluated by propagation of error of the mean (Bevington, 1969, p. 71). Given that the error measures are larger than the difference of the means, the slightly larger age-related loss for colour is not statistically significant. A three-way ANOVA of age, temporal frequency and stimulus (luminance or colour), revealed no significant interaction between age and stimulus F(2,100) = 0.5, P = 0.61.

Comparison of detection/discrimination thresholds

Many previous studies (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Mullen & Boulton, 1992; Derrington & Henning, 1993; Palmer *et al.*, 1993; Metha *et al.*, 1994; Gegenfurtner & Hawken, 1995) have shown a difference in discrimination/detection thresholds for chromatic stimuli, but the conditions under which this occurs vary greatly with exposure duration, temporal and spatial frequency and many other factors. To assess the difference in our particular conditions, we measured separately discrimination and detection thresholds for two young, well trained observers over a range of temporal frequencies. For luminance stimuli, detection



FIGURE 4. (A) Contrast sensitivity (mean values of two young subjects) as a function of temporal frequency for 1 c/deg drifting gratings, with either pure luminance contrast (circles) or pure colour contrast (triangles). The solid symbols represent sensitivity for detection, the open symbols discrimination of motion direction. (B) Ratio of detection to discrimination contrast sensitivity (in log units) for ten young and ten old subjects, for both luminance (open columns) and colour (hatched columns), measured at 2 Hz. The bars show the standard error of the mean.

was virtually identical to direction discrimination at all temporal frequencies [Fig. 4(A)]. However, for chromatic stimuli, detection was superior to discrimination at temporal frequencies <8 Hz, but similar at higher temporal frequencies.

Figure 4(B) replots data from Figs 2 and 3 to show the average ratios of detection to discrimination thresholds, for young and old subjects, for luminance (open columns) and colour (hatched columns) gratings drifting at 2 Hz. The fact that the ratios for both luminance and colour are very similar for old and young subjects suggests that the age-related deficit is not specific for motion mechanisms.

Pupil size

With ageing studies it is important to examine to what extent the observed effects may depend on the reduced pupil size brought about by senile miosis. We therefore measured representative thresholds for both detection and direction discrimination at 2 Hz, and for direction discrimination at 20 Hz as a function of pupil size in one trained subject. Figure 5 shows the results. Varying pupil diameters from 3 to 4.75 mm (changing area by a factor of 2.5) produced no measurable change in contrast sensitivity. The arrows on the abscissa indicate the average pupil size for the two age groups of this study, well contained within the experimental values. Clearly, the differences in sensitivity observed in this study cannot be explained by senile miosis.

Visual evoked potentials

Amplitude. Visual evoked potentials can provide useful information about visual performance above threshold. We therefore measured steady-state evoked potentials as a function of temporal frequency in two groups of subjects of mean ages 25.5 (ten subjects) and 71.5 (nine subjects). Two subjects of the first group and six of the second group had also participated in the psychophysical experiment.

In order to equate for the different cone-contrasts of luminance and chromatic stimuli, both stimuli were scaled in contrast for equal visibility. Contrast was set to ten times the detection threshold (colour or luminance) of 1 c/deg gratings, counterphased at 5 Hz (a temporal frequency that yields strong VEPs for both colour and luminance). In all the elderly subjects, the contrast at equiluminance corresponded to 90%, the maximum available with full linearity. We also measured thresholds as a function of colour ratio, to establish the equiluminant point of those who had not participated in the earlier study. Note that this technique for establishing equilu-



FIGURE 5. Contrast sensitivity of one subject for detection (○) and direction discrimination (●) with artificial pupils of different diameters. Stimulus temporal frequency: 2 Hz (top) or 20 Hz (bottom). The uppermost data are for luminance contrast sensitivity, all the other data are for colour contrast sensitivity. The arrows indicate mean pupil size for the young (open) and old (filled) subjects.



FIGURE 6. (A) and (B) Amplitude of second harmonic of steady-state VEPs (normalized to the average amplitude of each subject) as a function of temporal frequency of sinusoidal counterphase contrast modulation, for the two groups of subjects (○, young; ●, old). The luminance contrast of the yellow-black stimuli (A) was ten times contrast threshold (see text). The colour contrast of the red-green stimuli (B) was ten times threshold. Average contrast was: young 25% luminance, 79% colour; old 33% luminance, 90% colour. (C) and (D) Average phase of the second-harmonic of steady-state VEPs as a function of stimulus temporal frequency for the young (○) and old (●) subjects. The numbers indicate the slopes in msec (apparent latency) of the various portions of the regression lines, for data up to or above 10 Hz.

minance is slightly different from that for the psychophysical experiment (minimum sensitivity for flicker at 15 Hz), but yielded the same results in a control experiment.

Figure 6 (A and B) shows the average of amplitudes as a function of temporal frequency. Before averaging, the amplitudes were first normalized to an average of 1, separately for colour and luminance. The normalization removes overall differences in amplitude (that may result from unspecific physical sources), leaving only relative differences (although in practice the results averaged without normalization were very similar). The results show that there were few systematic age-related effects on VEP amplitude. Over most temporal frequencies, the average VEPs for old and young observers were similar to within 1 SE. The only obvious difference between the young and old observers was for equiluminant stimuli of high temporal frequencies. VEPs for the elderly group plummeted to noise level at 12 Hz, whereas those of the young group remained reliable up till 24 Hz.

Phase. To describe fully the steady-state VEP, one has to consider both amplitude and phase. The average

phases associated with the amplitudes of Fig. 6 (A and B) are shown in Fig. 6 (C and D) [see Porciatti *et al.* (1992) for details of ordering the phase plot]. As has been well documented previously, phases decrease monotonically with temporal frequency, and the slope of these functions provides an estimate of the apparent delay of the evoked potentials [see Regan (1966); Spekreijse *et al.* (1977)].

Inspection of the curves of Fig. 6 suggest that they may have two separate limbs, as has been reported before (Porciatti *et al.*, 1992; Morrone *et al.*, 1996). We therefore fitted the data (by linear regression) with two separate lines, for frequencies less than and greater than 10 Hz, the temporal frequency where the amplitude curve shows a secondary minimum (see Simon, 1992). Note that it was not possible to obtain a curve for the higher frequencies of equiluminant stimuli for the elderly group, as the potentials were not sufficiently reliable at the higher frequencies. The slopes of the curves (in msec) are indicated on the figure. For both young and old observers, the slopes were steeper for low temporal frequencies, suggesting longer apparent latencies over that range. For all conditions where the comparison was possible



FIGURE 7. Mean apparent latencies and standard errors of the VEPs of young (open columns) and old (hatched columns) subjects, derived from the regression lines of phase against temporal frequency of single subjects. The temporal frequency ranges over which the apparent latencies were computed are indicated above the bars.

(luminance condition of high and low temporal frequency and equiluminance of low temporal frequency), the apparent latency for the elderly group was slower, by about 30 msec.

The histogram of Fig. 7 shows similar results. These report estimates of apparent latency, obtained in a

slightly different way. Whereas Fig. 6 shows fits to data averaged over all observers, the slopes of Fig. 7 were obtained by fitting the data of individual observers with the two curves, and then averaging the estimates of slope (bars indicating standard errors). The two techniques yielded similar results, giving us confidence in the technique. Again, Fig. 7 shows an age-dependent increase in apparent latency of about 30 msec, similar for all three conditions.

Transient visual evoked potentials

For completeness, we also measured transient VEPs to square-wave (1 Hz) phase-reversal of the grating stimuli used for steady-state responses. As before, contrast was ten times detection threshold for both luminance and equiluminance patterns. In Fig. 8 transient VEPs of individual observers are shown without normalization by the thin lines, with the thick lines representing the group averages. It is obvious that there is considerable scatter in traces, possibly because of the low contrast.

Responses of young subjects to luminance contrast (upper left panel) show a major positive wave followed by a late negative wave. While the response amplitudes do not vary much across subjects, there is a noticeable jitter of the major positive peaks. This variability in peak



FIGURE 8. Transient VEPs of young (A, B) and old (C, D) subjects for stimuli modulated in luminance contrast (A, C) or colour contrast (B, D) and square-wave reversed in contrast at 1 Hz. Stimulus contrast ten times detection threshold (see text). Thin lines are single subject responses (at least 200 sums); heavy lines, waveforms averaged across subjects.

latency has probably to be ascribed to the different contrasts used for different subjects (as mentioned above, contrasts were scaled to threshold). As reported before (Fiorentini *et al.*, 1991), for young subjects the transient VEPs to colour contrast-reversal consist of a major negative wave (upper right panel). The transient VEPs of the elderly subjects do not differ substantially from those of the younger, apart from a tendency of the positive wave to split into two components both for the luminance and for the colour contrast responses.

DISCUSSION

The main results of the present work are the decline of sensitivity between 30 and 70 yr of age for both luminance contrast and colour contrast (about 0.3 log units) and an increase of the apparent latency of the VEPs in response to pattern reversal with age, again by a similar amount (both about 30 msec), for luminance and for colour contrast. The elevation of contrast thresholds for drifting gratings in the aged group was approximately the same for detection as for discrimination of motion direction of the grating, and largely independent of temporal frequency over the range investigated.

Since the effects of ageing were substantially the same for sensitivity to luminance and colour contrast, it is possible that they arise at a peripheral level. Among the possible optical factors is senile miosis, responsible for a lower retinal illuminance in the aged eyes. However, our control experiment indicated that the small reduction in pupil size observed in aged subjects did not induce an appreciable change in contrast sensitivity for either luminance or colour contrast. Other optical factors may contribute to the impairment of contrast sensitivity in the aged, notably the increase in the density of the optical media, and in particular of the lens, and the light scatter. The optical density of the lens is known to increase with age, particularly at the shorter wavelengths (Said & Weale, 1959; Ruddock, 1965). As noted before, this may explain the slight change in the equiluminance colour ratio in the aged with respect to the young subjects, with a higher proportion of green needed for the aged. The spectral content of our stimuli was limited to a range above 500 nm, where the wavelength dependence of optical density in the aged is not large and the overall increase in lens absorption with age is relatively small. Given these conditions, the age-related change in lens transmission as a function of wavelength [evaluated by van den Berg & Ijspeert (1995)], leads to a predicted average shift of the equiluminant point from 0.5 to about 0.45 for our older subjects, while the earlier data of Ruddock (1965) predict a shift to 0.48. Both these predictions agree reasonably well with the observed average shift in equiluminance points, but this is unlikely to contribute towards the decrease in sensitivity. In addition, the small decrease in mean retinal illuminance from lens yellowing is not likely to play a significant role in decreasing the contrast sensitivity of older eyes at the relatively low spatial frequency of our stimuli (Sloane et al., 1988).

A factor that may play a role in reducing contrast sensitivity is light scatter in the eye. Intraocular light scatter increases moderately with age in the absence of cataract and, more importantly for the present study, is largely independent of wavelength (Wooten & Geri, 1987; Whitaker et al., 1993; van den Berg & Ijspeert, 1995). Therefore it is reasonably safe to assume that the contrast of the two components of our stimuli, the gratings produced by the red and by the green gun, are reduced by approximately the same amount by light scatter. This in turn is important for the equiluminance settings, because it ensures that when changing the colour ratio, only the relative luminances of the red and green patterns are changed, the two contrasts being matched in the retinal images of the two gratings. Another possibility is that the relative sensitivities of the L and M cones, that provide the major response to our stimuli (as S cones are practically insensitive to wavelengths below 500 nm), are differentially affected by ageing processes. This does not seem to be the case, however. The loss in quantum efficiency of the cones as determined from the psychophysical absolute threshold (with adaptation conditions that isolate the responses of the three cones) is not large (about 0.1 log unit per decade) and is approximately the same for the three types of cones [see Werner et al. (1990) for review].

The contribution of optical factors may not account totally for the contrast sensitivity loss observed in our aged subjects. Indeed, there is general agreement that the loss of luminance contrast sensitivity with age results at least in part from neural factors (Morrison & McGrath, 1985; Burton et al., 1993; Artal et al., 1993). However, the mechanisms responsible for the ageing process are still largely unknown, as are the sites of the visual system that might be primarily involved (Spear, 1993). The unspecific loss of contrast sensitivity observed in the present experiments, both for colour and for luminance, for discrimination and for detection, does not suggest that any particular site or neural pathway may be more vulnerable, and hence preferentially influenced by the ageing process. The stimuli used in our experiments were chosen to reveal a possible selective contribution of different neuronal populations to the loss of contrast sensitivity with age. Indeed, for gratings drifting at a low temporal frequency (2 Hz) and of sufficiently long duration (gaussian window of half-width 200 msec) there is a large separation between thresholds for detection and thresholds for discrimination of motion direction for equiluminant red-green gratings, while the two thresholds are not differentiated for the gratings with pure luminance contrast. This should have favoured a differentiation of the effects of ageing for the various conditions tested, were these effects more pronounced for the mechanisms responsible for luminance than for colour contrast sensitivity (or vice versa). Current evidence from human and monkey experiments supports this view, suggesting the existence of two separate motion systems, one for low temporal frequencies, that is sensitive to colour, and another for high temporal frequencies that is mostly sensitive to luminance (Gegenfurtner *et al.*, 1994; Gegenfurtner & Hawken, 1995).

It is interesting to mention that in the monkey the contrast sensitivity for gratings of 1 c/deg drifting at a low temporal frequency is subserved by the P pathway, while the M pathway is responsible for luminance contrast sensitivity at higher temporal frequencies, in particular at 10 Hz (Merigan et al., 1991; Merigan & Maunsell, 1993). The sensitivity to colour contrast is ascribable purely to the P pathway (Merigan & Maunsell, 1993). Although the coloured stimuli used in the monkey experiment were different from ours, it is likely that the sensitivity for red-green colour contrast in our conditions is also primarily subserved by the P pathway. It would seem that ageing affects primarily mechanisms peripheral to the site where the P and M pathway differentiate, or that the two pathways are equally affected by the ageing process, at least as far as they are concerned with subserving contrast sensitivity.

The results of the VEP experiment confirm previous results showing an increase in the (apparent) latency of responses to reversal of luminance contrast with age [see Spear (1993) for review] and extend this result to the responses to colour contrast reversal. The amplitude of the responses indicates a selective loss at the higher temporal frequencies that agrees with the loss of temporal resolution with age reported in the literature (Tyler, 1989; Nameda et al., 1989). In the young subjects, the regression of phase against temporal frequencies shows a discontinuity around 10 Hz, for both luminance and colour contrast responses. The break around 10 Hz and the different slopes of the regression lines below and above 10 Hz is suggestive of the contribution of two populations of neurones with somewhat different temporal properties (Simon, 1992; Porciatti et al., 1992; Morrone et al., 1996). In our previous work about the effects of ageing on the properties of the retinal and cortical potentials evoked by luminance contrast reversal, we found that in aged, but not in young subjects, there was a break in the regression line of VEP phases against temporal frequency and we suggested that this might indicate a differential effect of ageing on different neuronal populations. This suggestion was reinforced by the fact that in the aged group the mean amplitude of the VEP responses was selectively reduced in the range of relatively low temporal frequencies.

While the results obtained from the aged subjects in the present work substantially replicate those of the previous experiment, those of the young group differ from the previous ones (showing here a break in the phase regression lines around 10 Hz) and in the present conditions the comparison between young and old subjects does not indicate selective effects of ageing for responses in different ranges of temporal frequencies (apart from a decrease in temporal resolution). The partial disagreement may be due to differences in the experimental conditions of the two experiments. The mean luminance available on the colour display in order

to produce equiluminant red–green stimuli was about ten times lower than the mean luminance of the black and white gratings used in the previous experiment (200 cd/ m^2). In the previous case, because of the need to record simultaneously PERG and VEP responses, the contrast of the stimuli was very high (90%) and equal for the two groups of subjects, while for the present work the contrast has been scaled to threshold in order to facilitate the comparison between the responses to luminance and colour contrast. Thus, the luminance contrast was much lower than in the previous work, especially for the young subjects (15–20%). This may justify the longer apparent latencies of the responses, particularly those observed for the young subjects in the range of low temporal frequencies.

The general finding of an increased apparent latency of the VEP responses with age is confirmed here and shown to be relatively unspecific for the type of stimulus, either luminance contrast of lower or higher temporal frequencies or chromatic contrast. This may reflect a ubiquitous slowing down of visual processes in the ageing neural system. The transient responses do show a tendency in the aged subjects for the main positive peak to split into two components, suggesting a more subtle modification of the temporal properties of cortical activity with age. However, the effect again is similar for luminance and colour contrast VEPs and it would be difficult to speculate on ageing processes underlying the (slight) changes in the waveform of transient responses. In any case, transient potentials evoked by low contrast stimuli are simply not reliable enough to permit excessive interpretation.

In conclusion, the present findings do not show any differential effect of ageing on the visual responses to patterns temporally modulated either in pure luminance contrast or in pure chromatic contrast, both at threshold and suprathreshold. The stimulus and experimental conditions were expected to favour differentially the contribution either of the P or of the M pathway to the responses, according to the data available from monkeys and to the current interpretation of human psychophysical experiments. The lack of differential effects of ageing in the various stimulus conditions tested, therefore, fails to provide evidence for a selective deterioration of either pathway.

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